

FREEZE-TOLERANCE OF CACTI (CACTACEAE) IN OTTAWA,
ONTARIO, CANADA

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ABSTRACT

Many fewer species of cacti are native to and thought to be able to survive winters in eastern Ontario than in the similarly cold winters of central Colorado. We collected 12 yr of data on 107 specimens representing 50 cactus species that have been tested outdoors in gardens in the City of Ottawa (Canada) and report which have successfully weathered six or more consecutive winters and which have not. Some species that we expected to be more successful were not, while a small number of species native to considerably warmer environments survived surprisingly well. We review general mechanisms for freeze-tolerance in plants, focusing on what is known about cacti in particular. Phylogeny does not appear to be important in determining success or failure in cold climates, so we explore other possible explanatory factors for differences in survival between Ontario and Colorado. Our data indicate that freeze tolerance of cacti in eastern Ontario may be a function of snow cover, rather than polyploidy. Colorado's greater cactus richness may also be a function of its location closer to the southwestern deserts' center of diversity, which would provide a larger pool of potential species that could expand to colder regions. More thorough studies of freeze-tolerance over a larger geographic range – albeit controlling for growing conditions, using identical clones at multiple sites, and determining precise cause of death – will be necessary to reach more definitive conclusions.

Key Words: Cactaceae, cold tolerance, freeze tolerance, polyploid, snow cover.

Cacti are native to the Americas, and are found largely in the deserts of the western Americas, with secondary diversification in eastern Brazil (Anderson 2001). Several species are found throughout eastern North America and the Caribbean and several species are native to Canada (Benson 1982; Bernshaw and Bernshaw 1984; Cota-Sánchez 2002; Hancock 2013). Cacti range from 50°S in Santa Cruz, Argentina (*Austrocactus bertinii* (E. Cels ex Hérincq) Britton & Rose, also see Mourelle and Ezcurra 1996) to 56°N in Alberta and British Columbia, Canada (*Opuntia fragilis* (Nutt.) Haw.) (Cota-Sánchez 2002; Gorelick 2015), while some cacti are found in habitats over 4000 m in elevation (Kiesling 1987). Freeze-tolerance should thus be expected, and indeed, many species in the cactus family (Cactaceae) are freeze-tolerant. A recent horticulture book by Leo Chance (2012) describes some 200 cactus taxa (which we reduce to 123

species here, as some are synonyms, subspecies, or varieties) that survive unprotected in cultivation in Colorado Springs, Colorado, with low temperatures each year being typically –25° to –30°C.

Typical winter temperatures in Ottawa, Canada, are similar to those in central Colorado. However, our current knowledge suggests only perhaps 20–30 cactus species can survive unprotected outdoors in Ottawa for at least five years. In fact, this number is smaller than the number of cacti that are native to the State of Colorado (approximately thirty). We compare several climate differences between eastern Colorado and eastern Ontario. We review reasons why only some species survive in the climate of eastern Canada. We first review mechanisms that plants, and specifically cacti, use to cope with severe winter conditions, e.g., low temperatures, freeze/thaw cycles, and levels of snow cover. We present twelve years of data on cacti surviving Ottawa winters, reporting those with better and worse

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survival and extend the list of species that can survive in Ottawa.

PHYSIOLOGICAL MECHANISMS THAT AID IN COLD TOLERANCE

Freeze-tolerance in most plants is usually via the same mechanism as dehydration-tolerance (Sakai and Larcher 1987; Close 1997; Thomashow 1999; Wharton 2002). Cold-hardening in plants often includes production of proteins related to dehydrins (Wharton 2002). Cold-hardening proteins in plants are at least sometimes homologous to proteins that provide pathogen resistance, especially against pathogenic fungi, but do not appear to be homologous with proteins that confer freeze-tolerance in animals (Griffith and Yaish 2004).

As temperatures cool in autumn, many plants move water out of cellular spaces. Extra-cellular water is typically without many solutes, so it freezes long before intra-cellular water. Furthermore there are often many nucleation centers in extra-cellular space (Wharton 2002; Vogel 2012).

Frozen water within cells can rupture membranes, putting the plant at risk of death. Plants take several approaches to keep intra-cellular water from freezing. Some plants are capable of supercooling, where water transitions from a liquid to a solid state at some temperature less than 0°C, but usually greater than -40°C (Gusta et al. 1983; Sakai and Larcher 1987; Vogel 2012). Supercooling does not protect the plant from damage if the temperature drops below the supercooling point, but can substantially extend freeze protection below 0°C.

Plant cells accumulate antifreeze solutes, especially in autumn, which lowers the freezing point of water (Sakai and Larcher 1987; Wharton 2002; Yadav 2010; Vogel 2012). High concentrations of solutes in cells and low concentrations outside of cells causes water to move to extra-cellular spaces, where it can safely freeze. The freezing point is also lowered in some plant cells by accumulation of unsaturated fatty acids and sugars (Sakai and Larcher 1987; Wharton 2002; Gusta et al. 2004) and possibly nucleic acids (Ken Storey, personal communication). Plant cells can and often manufacture their own sugars, lipids, proteins, and nucleic acids during cold acclimation.

"The major adverse effect of cold stress in plants has been seen in terms of plasma membrane damage. This has been documented due to cold stress-induced dehydration (Steponkus 1984; Steponkus et al. 1993). The plasma membrane is made up of lipids" (Yadav 2010, p. 517). In addition to the accumulation of unsaturated fatty acids in cell membranes, freeze tolerance is likely due to production of proteins that stabilize membranes. For some proteins, this

membrane stabilization seems to be due to altering membrane curvature, thereby lowering temperature of membrane phase transitions from lamellar to hexagonal II (Thomashow 1999). Lamellar membranes are a simple flat bilayer or a relatively even stack of multiple such bilayers, like a stack of pancakes. Hexagonal II membranes are a hexagonally packed array of lipid tubes in which each tube is a simple bilayer that is oriented perpendicularly to the previous lamellar membrane (Siegel and Eppand 1997).

Chen et al. (1983) claimed that freeze tolerant plants have elevated abscisic acid (ABA) levels for a day or so following cold acclimation, whereas more tender sister taxa do not. Furthermore, freeze-intolerant species become freeze tolerant when injected with ABA. However, Thomashow (1999) expressed doubts about the role played by ABA, due to the transient nature of the effect. Nonetheless there are hints that ABA affects lipid metabolism and thereby has an effect on membranes (Farkas et al. 1985).

Once most water is moved outside of cells, any remaining water in cells is usually tightly bound to the endoplasmic reticulum, so is not really freezable (Wharton 2002; Vogel 2012). Instead, such tightly bound water undergoes vitrification, i.e., becomes glass-like.

Freeze tolerance also can be a function of detoxification of reactive oxygen species (Yadav 2010), although we do not know the mechanisms by which free radicals are mopped up.

Freeze tolerance seems to be a quantitative trait due to many genes on all chromosomes. Freeze tolerance takes time – acclimation to colder but not very cold temperatures (Gusta et al. 2004). Transcript levels of freeze tolerance genes increase dramatically within 15 minutes of cold exposure for some genes and within two hours for others (Thomashow 1999).

COLD TOLERANCE IN CACTI

There is little literature specifically relating to freeze-tolerance in cacti, and most of that was out of Park Nobel's lab from 1980–1995 (Nobel 1980, 1981, 1982, 1988; Loik and Nobel 1991, 1993; Goldstein and Nobel 1994; Nobel et al. 1995) and their lab's method for inducing freezing was somewhat artificial. See Table 4.2 on page 107 of Nobel (1988) for a summary of low-temperature tolerances for 18 species of cacti. However, see the cautionary note on pages 1892–1893 of Ishikawa and Gusta (1996) regarding how Nobel's technique may have underestimated levels of cold-tolerance. Loik and Nobel (1993) estimated freeze-tolerance in environmental growth chambers and measured survival rates (LT₀ and LT₅₀) by staining chlorenchyma cells with neutral red dye. Ishikawa and Gusta (1996) estimated freeze-tolerance in natural conditions

and measured survival rate by looking for necrotic tissue. We do not attempt to establish methodological effectiveness here, but note that visible necrosis can take considerable time to become visible in freeze-damaged specimens of *Carnegiea gigantea* (Engelm.) Britton & Rose (Steenbergh and Lowe 1977).

If cold-hardening (an odd term insofar as the tissues don't always get physically harder; see the following paragraph) is applicable in cacti, these mechanisms should facilitate living in xeric environs. This highlights that the key to freeze-tolerance is properly dealing with water, possibly keeping intracellular water from freezing. Loss of water from cells is evident in many cacti in winter, such as the relatively flaccid shoots in freeze-tolerant species of *Opuntia* Mill., *Cylindropuntia* (Engelm.) F.M. Knuth, and *Echinocereus* Engelm. However shoots of other freeze-tolerant cacti remain relatively turgid in winter, such as species of *Pediocactus* Britton & Rose and *Maihuea* Phil. Supercooling has not been documented in cacti, but might be sufficient to prevent damage in Ottawa, where the lowest temperatures usually are only around -30°C to -35°C.

The hardening aspects of cold-hardening have been quantified in *Opuntia fragilis* (Nutt.) Haw. (Ishikawa and Gusta 1996). Between 6 September and 10 October, they lowered ambient temperature from -7°C to -50°C. On 6 September, water content was 5.38% of dry weight of cladodes; on 10 October water content was 2.63% of dry weight – a diminution of roughly half the water – and cladode diameter was reduced by 30%.

Vitrification must be at play in the far-northern prickly pear *Opuntia fragilis* because shoots successfully weathered an hour in liquid nitrogen, at -196°C after the plant had been cold-acclimated to -40°C (Luyet and Thoennes 1938; Ishikawa and Gusta 1996).

Opuntia ficus-indica (L.) Mill. produces cold-shock proteins (Somers et al. 1991). This is an indication that such proteins occur in other cacti, at least in opuntioids, especially since *O. ficus-indica* is not very cold tolerant, perishing to about -9°C (Nobel 1988).

Freeze-tolerance can also be drastically different between populations. The temperature at which half the cladodes of *O. polyacantha* Haw. died (LT₅₀) was -17°C from a population in southern Wyoming (Nobel 1982) and -55°C for a population from Saskatchewan (Ishikawa and Gusta 1996). However, these two different LT₅₀ values may be due to different methods for measuring freeze-tolerance.

Below, we report freeze-tolerance for cacti as a binary variable – did plants survive winters or not – for a pair of sites in the city of Ottawa over several years. We have not tried to ascertain specific cause of death (e.g., cells lysing, extensive

microbial infestations in wet springs, etc.). While beyond the scope of this paper, a more thorough study might examine multiple clones cultivated across multiple geographic locations in North America, all sites with the identical soils, light exposure, and even similar overhead effects from nearby trees and buildings that can ameliorate radiation frost (a.k.a. hoarfrost) (Jordan and Smith 1995).

DATA AND ANALYSES

A variety of species are already known to survive in Ottawa including the native Canadian species (*Coryphantha vivipara*, *Opuntia* × *columbiana*, *O. fragilis*, *O. humifusa*, *O. polyacantha*). We carried out a preliminary assessment of survival on 50 species, planting 107 specimens and documenting year of death over a period of twelve years. Two of us (RG, KH) live in Ottawa and have carried out the plantings and maintenance of the described taxa, and here we report which species were more or less successful surviving Ottawa's winters (Table 1). In many cases we confirmed that infraspecific ranks (subspecies, variety) of a given species are also hardy in Ottawa. We also confirmed the hardness of all native Canadian species as able to live in Ottawa, with plant material derived from several native habitats (Hancock 2013). We largely follow the nomenclature of the *Flora of North America* (Parfitt and Gibson 2003) and the *New Cactus Lexicon* (Hunt et al. 2006). Freeze-tolerant cacti in Ottawa include the following species, which have each weathered at least six successive winters:

Maihueoidiaceae

- Maihuea patagonica* Britton & Rose
- Maihuea poeppigii* F.A.C. Weber

Opuntioideae

- Cylindropuntia imbricata* (Haw.) F.M. Knuth
- Cylindropuntia whipplei* (Engelm. & J.M. Bigelow) F.M. Knuth
- Opuntia arenaria* Engelm. [= *O. polyacantha* var. *arenaria* (Engelm.) B.D. Parfitt]
- Opuntia aurea* E.M. Baxter
- Opuntia* × *columbiana* Griffiths (pro. sp.)
- Opuntia fragilis* (Nutt.) Haw.
- Opuntia humifusa* Raf.
- Opuntia macrorhiza* Engelm.
- Opuntia phaeacantha* Engelm.
- Opuntia polyacantha* Haw.
- Opuntia tortispina* Engelm. & J.M. Bigelow [= *O. cymochila* Engelm. & J.M. Bigelow]

Cactoideae

- Coryphantha sneedii* (Britton & Rose) A. Berger
- Coryphantha vivipara* (Nutt.) Britton & Rose

Echinocereus reichenbachii (Terscheck) Britton & Rose

Echinocereus triglochidiatus Engelm.

Pediocactus knowltonii L.D. Benson

Pediocactus simpsonii (Englem.) Britton & Rose

Pediocactus winkleri K.D. Heil

Where known, Table 1 provides geographic locality information for where seeds or cladodes were collected and plant collector field numbers. This gives some indication of minimum winter temperatures and cumulative annual snowfall in the plant's native ranges, which may be particularly important for wide-ranging species such as *Opuntia fragilis*, *O. polyacantha*, *O. humifusa*, *Coryphantha vivipara*, and *Pediocactus simpsonii*, the first four of which are native to Canada as well as the southwestern U.S. Collection numbers may be useful because we subsumed several varieties under the more inclusive species rank. For example, we subsumed under *Pediocactus simpsonii* the following varieties: *Pediocactus simpsonii* var. *indraianus* Hochstätter, *P. simpsonii* var. *minor* Cockerell, *P. simpsonii* var. *nigrispinus* Hochstätter, and *P. simpsonii* var. *robustior* (J.M. Coulter) Hochstätter. Readers wishing to segregate out varieties and subspecies of many of the species we report will be able to do so using the collection numbers (see for example, Christophe Ludwig's website <http://cludwigfr.dyndns.org/contact.asp?Lang=en> or Ralph Martins website <http://ralph.cs.cf.ac.uk/Cacti/fieldno.html>) and location of origin data we present in Table 1. This table also lists species that did not survive multiple winters in Ottawa.

Table 1 provides additional information on what year individual plants were first grown outdoors in Ottawa and during which winter they perished. Each individual plant, likely different clones, is represented by a separate line. We do not have information on geographic origin nor collection number for many of these plants.

The species evaluated in this paper were all grown in the Ottawa suburban gardens of two of us (RG and KH), one in the Alta Vista subdivision (south central Ottawa) and one in the Ryan Farm sub-division (in the west Ottawa ward of Nepean). In both gardens, plants grew on well-drained sand and were not protected in any way, at any time. However any leaves that blew onto them in the fall were removed before winter to preclude rot during winter or spring thaws. The cacti were left to grow naturally and were not fertilized, watered, nor covered. Those in the Alta Vista sub-division were in a single raised open bed of 30 cm of medium grained sand with access to the sun for most of the day, save for occasional shade of surrounding sugar maples. The garden in the Ryan Farm sub-division had two hardy cactus beds. One is south

facing and adjacent to an unheated garage on a slope to the east. The second in the Ryan Farm subdivision was a raised west facing bed on level ground, adjacent to an unheated shed. Both beds had good access to the sun.

Some cacti have been identified, either in the literature or anecdotally, as being freeze-tolerant at temperatures commonly considered to be typical of Ottawa winters (e.g., -25° to -30°C), yet we have not found all of those to be successful in Ottawa. Often we have made multiple attempts to grow a given species without success, thus documenting the winter demise of specimens considered to be potentially freeze-tolerant.

We also compared winter climate differences between Ottawa, Canada, and eastern Colorado (Plant Hardiness Zone 5), the region of interest highlighted by Chance (2012). We obtained data for Ottawa MacDonald-Cartier International Airport (45.3225°N, 75.6692°W, at 114 m elevation) from Environment Canada. For Colorado, we obtained data for Colorado Springs Municipal Airport, CO US (38.810°N, 104.688°W, at 1884 meters elevation) from the National Climatic Data Center (NCDC, NOAA). For both locations we obtained data for Monthly Climate Normals from 1981–2010 (Table 2).

Mean minimum daily temperatures are a few degrees colder in Ottawa than Colorado Springs, with a nearly 7°C gap in January (Table 2). Minimum temperatures at both locations fall below freezing nearly every day during the winter months. Perhaps the most dramatic difference in the climate of these two locations is the difference in snowfall and resulting accumulation. Colorado Springs receives (on average) less than 15 cm of snow during each of December, January, and February, while Ottawa receives over 50 cm, on average, in December and in January, and over 40 cm in February, resulting in very few days with appreciable snow cover in Colorado Springs (Table 2). In Ottawa, appreciable snow accumulation occurs in well over 50% of days during these three months. The wetness of the snow in Ottawa versus Colorado Springs is difficult to judge, particularly as it is highly variable throughout a season, across storms, and across years. Colorado may have 20:1 events (20 cm of snow to one cm of water), or 8:1 events, and Ottawa has even wetter snow events. The likely gross averages are perhaps 15:1 in Colorado Springs and 12:1 in Ottawa, with Ottawa having wetter snow.

Not only should winter precipitation matter, but also so might summer precipitation. Most cacti are native to regions with summer rains. However, a few are from areas with mostly winter precipitation. The two species of *Maihuea* provide a tantalizing anecdotal example. While both species survive in Ottawa, a place in which all seasons are wet, *M. poeppigii* grows far more

TABLE 1. CACTI TESTED IN OTTAWA AND NUMBER OF WINTERS SURVIVED. **Bold face font** refers to plants that survived at least one full winter, and are considered **hardy** in Ottawa. All species in regular face font are considered not hardy in Ottawa. Several additional specimens survived more than five winters, however the exact dates are unavailable and denoted with *NR* (no record). Geographic origins and collection numbers, where known, are listed. Each reported line in Table 1 represents what we believe to be a different clone. All species but *Maihuenia* are from the U.S. or Canada, for which we omitted the name of the country and abbreviated the state/province. Collections (if available) are given with initials of the collector (first last) and collection number. Collector initials are for the following individuals: Bill Beaton (BB), J. R. Thompson (JRT), Eberhard Lutz (LZ), Ralph Peters (RP), Gary Loos (GL), and Steve Brack (SB). Where information was not available for geographic origin this is noted with *unknown*. When collection information is lacking, this is noted as *none*.

Subfamily	Taxon	Geographic origin	Collector, Collection Number	Year planted	Winter of death	Died in winter number
Maihuenioidae	<i>Maihuenia patagonica</i> (Phil.) Britton & Rose	Sierra Grande, Río Negro, Argentina	<i>none</i>	2007	alive 2014	>5
	<i>M. poeppigii</i> (Otto & Pfeiff.) F.A.C. Weber ex K. Schum.	Volcan Antuco, Bio Bio (Region VIII), Chile	<i>none</i>	2008	alive 2014	>5
	<i>M. poeppigii</i>	unknown	<i>none</i>	2001	2001–2002	1
	<i>Austrocylindropuntia subulata</i> (Muehlenpf.) Backeb.	unknown	<i>none</i>	2008	2009–2010	2
	<i>Corynophuntia clavata</i> (Engelm.) F.M. Knuth	unknown (but endemic to central NM)	<i>none</i>	2006	2006–2007	1
	<i>C. parishii</i> (Oreutt) F.M. Knuth	west of Cameron, AZ	LZ 267	2007	2007–2008	1
	<i>C. schottii</i> (Engelm.) F.M. Knuth	unknown	<i>none</i>	2008	2010–2011	3
	<i>Cylindropuntia davisii</i> (Engelm. & J.M. Bigelow) F.M. Knuth	unknown	<i>none</i>	1999	1999–2000	1
	<i>C. davisii</i>	unknown	<i>none</i>	2001	2003–2004	3
	<i>C. echinocarpa</i> (Engelm. & J.M. Bigelow) F.M. Knuth	unknown	<i>none</i>	2013	2013–2014	1
	<i>C. imbricata</i> (Haw.) F.M. Knuth	unknown	<i>none</i>	2004	2008–2009	>5
	<i>C. imbricata</i>	unknown	<i>none</i>	2009	alive 2014	>5
	<i>C. imbricata</i>	unknown	<i>none</i>	2001	2002–2003	2
	<i>C. imbricata</i>	unknown	<i>none</i>	2000	2003–2004	4
	<i>C. imbricata</i>	unknown	<i>none</i>	1999	1999–2000	1
	<i>C. kleiniae</i> (DC.) F.M. Knuth	unknown	<i>none</i>	2006	alive 2014	>5
	<i>C. leptocaulis</i> (DC.) F.M. Knuth	Las Cruces, Doña Ana Co., NM	<i>none</i>	2003	2006–2007	1
	<i>C. leptocaulis</i>	unknown	<i>none</i>	2010	2010–2011	1
	<i>C. prolifera</i> (Engelm.) F.M. Knuth	unknown	<i>none</i>	2013	2013–2014	1
	<i>C. versicolor</i> (J.M. Coulter) F.M. Knuth	unknown	<i>none</i>	2007	2007–2008	1
	<i>C. × viridiflora</i> F.M. Knuth	Santa Fe, NM	<i>none</i>	1999	1999–2000	1
	<i>C. × viridiflora</i>	unknown	<i>none</i>	2000	2002–2003	3
	<i>C. whipplei</i> (Engelm. & J.M. Bigelow) F.M. Knuth	unknown	<i>none</i>	2007	alive 2014	>5
	<i>C. whipplei</i>	unknown	<i>none</i>	2001	2002–2003	2
	<i>C. whipplei</i>	unknown	<i>none</i>	2001	2003–2004	3
	<i>C. whipplei</i>	unknown	<i>none</i>	2001	2001–2002	1
	<i>C. whipplei</i>	unknown	<i>none</i>	1999	1999–2000	1
	<i>Opuntia arenaria</i> Engelm.	El Paso Co., TX	<i>none</i>	2004	2010–2011	>5
	<i>O. arenaria</i>	unknown	<i>none</i>	2004	2005–2006	2
	<i>O. arenea</i> E.M. Baxter	unknown	<i>none</i>	2007	alive 2014	>5
	<i>O. basilaris</i> Engelm. & J.M. Bigelow	unknown	<i>none</i>	2004	alive 2014	>5
	<i>O. basilaris</i>	unknown	<i>none</i>	1999	1999–2000	1
	<i>O. basilaris</i>	unknown	<i>none</i>	2001	2003–2004	2

TABLE 1. Continued.

Subfamily	Taxon	Geographic origin	Collector, Collection Number	Year planted	Winter of death	Died in winter number
Cactoideae	<i>O. basilaris</i>	unknown	none	2008	2010–2011	3
	<i>O. × columbiana</i> Griffiths (pro sp.)	Cache Creek, BC	none	1997	alive 2014	>5
	<i>O. fragilis</i> (Nutt.) Haw.	Kaladar, ON	none	2006	alive 2014	>5
	<i>O. fragilis</i>	Lake of the Woods, ON	none	2006	alive 2014	>5
	<i>O. fragilis</i>	Lauder Sandhills, MB	none	2006	alive 2014	>5
	<i>O. fragilis</i>	Dunvegan, AB	none	2006	alive 2014	>5
	<i>O. fragilis</i>	Peace River, AB	none	2008	alive 2014	>5
	<i>O. fragilis</i>	S end of Kilpoola Lake, W of Osoyoos, BC	none	2009	alive 2014	>5
	<i>O. fragilis</i>	Mt. Kobau, 15 km NW of Osoyoos, BC	none	2009	alive 2014	>5
	<i>O. fragilis</i>	Keremeos, BC	none	2009	alive 2014	>5
	<i>O. fragilis</i>	northern CO [prob. Boulder Co.]	none	2006	alive 2014	>5
	<i>O. humifusa</i> (Raf.) Raf.	Point Pelee National Park, ON	none	1997	alive 2014	>5
	<i>O. macrohiza</i> Engelm.	unknown	none	2002	2012–2013	>5
	<i>O. microdasys</i> (Lehm.) Pfeiff.	unknown	none	2006	2006–2007	1
	<i>O. microdasys</i>	unknown	none	2005	2005–2006	1
	<i>O. phaeacantha</i> Engelm.	unknown	none	2001	2002–2003	2
	<i>O. phaeacantha</i>	unknown	none	2000	2006–2007	7
	<i>O. phaeacantha</i>	unknown	none	1999	1999–2000	1
	<i>O. polyacantha</i> Haw.	Jenner, AB	none	2006	alive 2014	>5
	<i>O. polyacantha</i>	Columbia River, WA	none	2002	2003–2004	2
	<i>O. polyacantha</i>	UT	none	2004	2006–2007	3
	<i>O. tortispina</i> Engelm. & J.M. Bigelow	Hartley Co., TX	SB 1047	2004	2004–2014	>5
	<i>O. violacea</i> Engelm. ex B.D. Jacks.	unknown	none	2006	2006–2007	1
	<i>Tephrocactus verschaffeltii</i> (F. Cels ex F.A.C. Weber) D.R. Hunt & Ritz	unknown	none	2008	2008–2009	1
	<i>Coryphantha dasycantha</i> (Engelm.) Orcutt	Brewster Co., TX	none	2007	2007–2008	1
	<i>C. minima</i> Baird	Brewster Co., TX	SB 968	2007	2007–2008	1
	<i>C. missouriensis</i> (Sweet) Britton & Rose	Oak Grove [Montrose, Montrose Co.], CO	none	2008	2008–2009	1
	<i>C. missouriensis</i>	unknown	none	2011	2011–2012	1
	<i>C. missouriensis</i>	Oak Grove [Montrose, Montrose Co.], CO	GL 48	2005	2006–2007	2
	<i>C. missouriensis</i>	unknown	none	2007	2007–2008	1
	<i>C. sneedii</i> (Britton & Rose) A. Berger	Organ Mts, Doña Ana Co., NM	SB 823	2007	alive 2014	>5
	<i>C. sneedii</i>	Doña Ana Co., NM	SB 173	2010	2011–2012	2
	<i>Coryphantha sneedii</i> var. <i>leei</i> (Boed.) L.D. Benson	Eddy Co., NM	SB 397	2005	2005–2006	1
	<i>C. vivipara</i> (Nutt.) Britton & Rose	Kyle Canyon, Clark Co., NV	RP 48	2007	alive 2014	>5
	<i>C. vivipara</i>	Colfax Co., NM	JRT 15171	2008	alive 2014	>5
	<i>C. vivipara</i>	Oak Lake, MB	none	2004	alive 2014	>5
	<i>C. vivipara</i>	Southern SK	none	2004	2010–2011	>5
	<i>C. vivipara</i>	unknown	none	1998	2001–2002	4
	<i>C. vivipara</i>	unknown	none	2000	2003–2004	4

TABLE 1. Continued.

Subfamily	Taxon	Geographic origin	Collector, Collection Number	Year planted	Winter of death	Died in winter number
<i>C. vivipara</i>	<i>C. vivipara</i>	unknown	none	2000	2003–2004	4
	<i>C. vivipara</i>	unknown	none	2004	2005–2006	2
	<i>C. vivipara</i>	near Bagdad, AZ	none	2006	2006–2007	1
	<i>C. vivipara</i>	Kaibab Plateau, Coconino Co., AZ	SB 906	2011	2011–2012	1
	<i>Echinocactus polycephalus</i> Engelm. & J.M. Bigelow	unknown	none	2008	2008–2009	1
	<i>E. polycephalus</i>	unknown	none	2007	2007–2008	1
	<i>Echinocereus dasycanthus</i> Engelm.	San Miguel Co., NM	SB 870	2005	2005–2006	1
	<i>E. davisi</i> Houghton (= <i>E. viridiflorus</i> var. <i>davisi</i> (Houghton) W.T. Marshall)	unknown	none	2008	2008–2009	1
	<i>E. engelmannii</i> (Parry ex Engelm.) Lem.	northern Navajo Co., AZ	SB 844	2010	2010–2011	1
	<i>E. reichenbachii</i> (Terscheck) Britton & Rose	unknown	none	2006	2007–2008	2
<i>E. viridiflorus</i>	<i>E. reichenbachii</i> var. <i>baileyi</i> (Rose) N.P. Taylor	unknown	none	2002	2004–2005	3
	<i>E. reichenbachii</i> var. <i>baileyi</i>	unknown	none	2006	2006–2007	1
	<i>E. reichenbachii</i> var. <i>perbellus</i> (Britton & Rose)	Timpas, Otero Co. CO	RP 121	2007	2007–2008	1
	L.D. Benson					
	<i>E. reichenbachii</i> var. <i>perbellus</i>	OK	none	2010	2010–2011	1
	<i>E. triglochidiatus</i> Engelm.	Mesa Co., CO	SB 686	2007	alive 2014	>5
	<i>E. viridiflorus</i> Engelm.	Taos Co., NM	SB 170	2005	2006–2007	2
	<i>E. viridiflorus</i>	unknown	none	2006	2006–2007	1
	<i>E. viridiflorus</i>	unknown	none	2008	2008–2009	1
	<i>E. viridiflorus</i>	unknown	none	2006	2006–2007	1
<i>P. simpsonii</i>	<i>E. viridiflorus</i> subsp. <i>chloranthus</i> N.P. Taylor	Manzano Mtns, Torrance Co., NM	SB 86	2005	2005–2006	1
	<i>Mammillaria wrightii</i> Engelm.	Emery Co., UT	SB 989	2007	2008–2009	2
	<i>Pediocactus despainii</i> S.L. Welsh & Goodrich	northern San Juan Co., NM	SB 304	2007	alive 2014	>5
	<i>P. sileri</i> (Engelm. ex J.M. Coult.) L.D. Benson	Antelope Valley, Mojave Co., AZ	RP 118	2007	2008–2009	2
	<i>P. simpsonii</i> (Engelm.) Britton & Rose	Yakima Co., WA	RP 05	2007	alive 2014	>5
	<i>P. simpsonii</i>	Laramie Plains, WY	SB 877	2007	alive 2014	>5
	<i>P. simpsonii</i>	Humboldt Co., NV	SB 1590	2007	alive 2014	>5
	<i>P. simpsonii</i>	Salmon, Lemhi Co., ID	RP 93	2007	alive 2014	>5
	<i>P. simpsonii</i>	Pueblo Peak, OR	BB 92–4	2007	alive 2014	>5
	<i>P. simpsonii</i>	plains of El Paso Co., CO	RP 106	2007	alive 2014	>5
<i>P. winkleri</i>	<i>P. simpsonii</i>	Western WA	none	2007	alive 2014	>5
	<i>P. simpsonii</i>	Colockum Pass, near Wenatchee, WA	none	2007	alive 2014	>5
	<i>P. simpsonii</i>	unknown	none	2000	2001–2002	2
	<i>P. simpsonii</i>	Wayne Co., UT	RP 103	2008	2001–2002	2
	<i>Sclerocactus brevispinus</i> K.D. Heil & J.M. Porter	Duchesne Co., UT	SB 1743	2007	alive 2014	>5
	<i>S. parviflorus</i> Clover & Jotter	San Juan Co., UT	RP 29	2007	2007–2008	1
	<i>S. parviflorus</i>	unknown	none	2008	2008–2009	1
	<i>S. pubispinus</i> (Engelm.) L.D. Benson	unknown	none	2006	2008–2009	3
	<i>S. pubispinus</i>	Millard Co., UT	RP 129	2008	2008–2009	1
	<i>S. spinosior</i> (Engelm.) D. Woodruff & L.D. Benson	Beaver Co., UT	SB 693	2007	2007–2008	1

TABLE 2. COMPARISON OF WINTER CONDITIONS IN OTTAWA (ONTARIO, CANADA) AND COLORADO SPRINGS (COLORADO, UNITED STATES) FROM CLIMATE NORMALS FOR THE PERIOD 1981–2010. Temperatures are given in degrees Celsius (°C) and snowfall and snow depth in cm. Because the Ottawa data come from Environment Canada, which reports values in cm for snow depth, while Colorado data come from the National Climatic Data Center which reports values in inches, the lower half of the table shows values for mean number of days with snow depths greater than 5 and 10 cm for Ottawa, while we provide number of days with snow depth greater than 7.6 cm (3 inches) for Colorado Springs (the two inch threshold is not provided in the normals output) for comparison. We also provide the frequencies for the even lower threshold of greater than 1 inch (2.5 cm) for Colorado Springs for comparison. The latitude and longitude and other station information for both sites are provided in the text.

Variable	Ottawa	Colorado Springs
Mean Min Daily Temp (°C)		
Dec	−10.1	−8.1
Jan	−14.8	−7.9
Feb	−12.8	−6.9
Mean number days Min ≤ 0°C		
Dec	29.6	29.6
Jan	30.1	29.7
Feb	27.1	26.5
Mean Monthly Snowfall (cm)		
Dec	52.5	14.5
Jan	53.9	14.2
Feb	43.3	12.4
Mean number days with snow depth:	≥5 cm (≥10 cm)	≥2.5 cm (≥7.6 cm)
Dec	19.7 (15)	6.4 (2.2)
Jan	29 (25.4)	5.6 (1.7)
Feb	27.3 (25.6)	4.3 (1.3)

vigorously in Ottawa than does *M. patagonica*. In their native habitats, *M. poeppigii* comes from areas of summer rains and often grows along rivulets, whereas *M. patagonica* is never remotely riparian and grows in areas with almost no summer rains (Roberto Kiesling, personal communication). This highlights a weakness of only examining the binary variable of survival in gauging cold-tolerance. Below, we discuss other explanations for differences in richness of cactus species that survive in Colorado versus Ottawa.

PHYLOGENY

The cactus species that survive unprotected in Ottawa represent three of the four subfamilies of the Cactaceae (Maihuenioideae, Opuntioideae, and Cactoideae, Table 1), so it is unlikely that there is phylogenetic signal in freeze-tolerance in Ottawa. The fourth subfamily, Pereskioideae, is monogeneric and fairly tropical, and no species of this group survive either in Colorado or Ottawa. Lack of phylogenetic signal seems typical for freeze-tolerance in animals as well, in which animal species with relatives from milder climates survive in surprisingly cold environments, i.e., it is high impossible to predict freeze-tolerance of a given animal species by knowing freeze-tolerance or lack thereof of related species (Ken Storey, personal communication).

SIZE, FREEZE TOLERANCE, AND SNOW COVER

There are some massive cacti that regularly survive freezing, especially some of the ceroid species in the Andean foothills, such as *Trichocereus atacamensis* (Phil.) W.T. Marshall & T.M. Bock subsp. *pasacanus* (F.A.C. Weber ex Rümpler) F. Ritter, *Trichocereus poco* Backeberg, and the somewhat smaller *Oreocereus celsianus* (Salm-Dyck) A. Berger ex Riccob., which survive above 4000 m elevation. The cacti that survive in Ottawa are much less massive, but may still be as much as 1.5 m tall (e.g., *Cylindropuntia imbricata*). The larger size and mass of these species may be advantageous to surviving colder conditions generally (Nobel 2002). While not quite as large, *Pediocactus simpsonii* shoots can be softball sized and *Maihuenia* clumps can grow to over a meter in diameter. Other species that survive in Ottawa are truly diminutive, such as *Pediocactus knowltonii* and *P. winkleri*. Size does not seem to be a limiting factor in whether cacti can survive the cold and wet environs of eastern Canada.

Some northern *Opuntia* species may grow lower to the ground (more decumbent) in order to benefit from a covering of snow, which ameliorates extreme ambient temperatures (e.g., Cota-Sánchez 2002). Freeze-thaw cycles may also contribute to death. Given that all species that survived in Ottawa were low-lying, except *Cylin-*

dropuntia spp., snow cover may be promoting survival. In subtropical deserts, many cacti rely on nurse plants for protection from cold weather (Drezner and Garritty 2003). The importance of nurse associations for cacti in Canada are not well known (though heavy shade is detrimental [VanDerWal et al. 2007]). Nurse plants can localize rain waters vis-à-vis drip lines and provide protection from radiation frost.

Two species surprised us by their freeze tolerance in Ottawa: *Coryphantha sneedii* and *Opuntia arenaria*. Both are from the Franklin and Organ Mountains between El Paso, Texas and Las Cruces, New Mexico, which is not a particularly cold or snowy region. Why there are not more species native to southern Ontario (such as low-lying ones) is unclear. Perhaps there is still too little snow cover and temperatures too low in some areas. The reason for lack of native cacti in Ottawa and in Canada is unclear, though the lower temperatures are likely compensated for by greater snow coverage and protection for low-lying species. Even *Cylindropuntia imbricata* is mostly or entirely snow covered for much of Ottawa's winters.

PLOIDY, RANGE AND GEOGRAPHY

The most freeze-tolerant cactus seems to be *O. fragilis*, which is also native to the most northern habitats. This species probably has the largest range of any cactus (excepting the epiphytic *Rhipsalis baccifera* (Sol.) Stearn, the only cactus to have made it to the eastern hemisphere possibly without the aid of humans). Cold acclimated *O. fragilis* easily survives -50°C , and half the cladodes survive both -70°C for one hour without cold acclimation and, after cold acclimation, for one-hour of immersion at -196°C (Ishikawa and Gusta 1996). All cladodes of *O. polyacantha*, which has a slightly smaller range than *O. fragilis*, survived at -40°C and half survived at -55°C (Ishikawa and Gusta 1996).

Opuntia fragilis and *O. polyacantha* tolerate a large range of climatic conditions evidenced by their extensive geographic ranges. Their tolerance to extreme temperatures appears to be better developed than their tolerance to precipitation variability. Habitat niche modeling for *O. fragilis* suggests that large fluctuations in precipitation may be limiting its distribution (Majure and Ribbens 2012). Some Canadian opuntiods, which are all in *Opuntia*, are native to counties with somewhat higher rainfall than typical for cacti. However, the native opuntiods of Canada generally show a preference for dry microsites. *Opuntia humifusa* has been studied in various populations and is consistently found in sandy and well-drained soil and xeric microsites and in areas with relatively high light levels (it tends to be less successful in more shaded areas), as has

been documented throughout its range such as in Florida (Abrahamson and Rubinstein 1976; Greenberg et al. 1994), Tennessee (Baskin and Baskin 1977), New Jersey (Hanks and Fairbrothers 1969), and Ohio (Jennings 1908; Noelle and Blackwell 1972). Similarly, in southeastern Manitoba, Canada, *O. fragilis* is associated with bare soil and xeric to highly xeric conditions, and areas with high light intensity (Frego and Staniforth 1985, 1986) and is found in high light microsites and on well-drained substrate, including granitic outcrops in disjunct populations (including the Kaladar, Ontario population), despite its distribution in short or mixed grass prairie in the more central portions of its range (Staniforth and Frego 2000). *Opuntia polyacantha* is also distributed in relatively dry microsites in the prairies, as is *Coryphantha vivipara* (Coupland 1950; Maw and Molloy 1980). Thus, while they are broadly distributed in humid climates, they are most successful in sunny dry habitats. Further, although *Opuntia* species are CAM photosynthesizers, *O. humifusa* stomata are open more when humidity is higher (Conde and Kramer 1975).

While our focus is on the colder/polar portion of ranges, we would be remiss to not mention that there are equally warm/equatorial range limits for these cactus species. Despite several attempts, one of us (RG) could never cultivate any species of *Pediocactus* in Tempe, Arizona. This makes it even more remarkable that *Coryphantha sneedii* – collections that were native to the area between El Paso, Texas and Las Cruces, New Mexico – seem to thrive in cultivation in the two low elevation environments of Tempe, Arizona and Ottawa, Ontario. Although, to our surprise, the higher elevation subspecies *C. sneedii* var. *leei* [SB 397] did not survive in either of our yards. Similarly, the most northerly cactus, *Opuntia fragilis*, which has been collected as far as $56^{\circ}17'\text{N}$ near the Beaton River east-northeast of Fort St. Johns, British Columbia (Gorelick 2015) is also native at least as far south as $36^{\circ}20'\text{N}$ in the grasslands of the Texas panhandle (Benson 1982). *Opuntia fragilis* has also been documented as surviving unprotected in cultivation as far north as Ivalo, Finland at $68^{\circ}40'\text{N}$ (Persson 1991). *Opuntia polyacantha* has a similarly large native range, from $52^{\circ}26'\text{N}$ near Unity, Saskatchewan to $30^{\circ}18'\text{N}$ in north-western Brewster County, Texas (Benson 1982), but seemingly not in Mexico (Pinkava 2004, unless one counts *Opuntia arenaria* as a variety of *O. polyacantha*).

Only five cactus species are native to Canada: *Coryphantha vivipara*, *Opuntia* \times *columbiana*, *O. fragilis*, *O. humifusa*, and *O. polyacantha* (Bernshaw and Bernshaw 1984; Cota-Sánchez 2002) (although, oddly, neither paper lists *O.* \times *columbiana* as being native to Canada). *O. fragilis*

is usually hexaploid (Pinkava et al. 1977, but see next paragraph); *Coryphantha vivipara* is tetraploid (Pinkava et al. 1992); *O. humifusa* is usually tetraploid (Marcucci and Tornadore 1997, but see next paragraph); *O. polyacantha* is diploid (Powell and Weedin 2001); we have not seen chromosome counts for *O. × columbiana* (Goldblatt and Johnson 1979–present, 2010). Polyploidy is relatively rare in cacti and, in fact, polyploidy is not known from the other fourteen species that survive Ottawa winters (Goldblatt and Johnson 1979–present, 2010). There is a tenuous positive correlation between freeze-tolerance and ploidy levels (Cota-Sánchez 2002).

Recent work shows that *O. humifusa* is diploid in the more southern parts of its range, as is *O. fragilis* (Majure et al. 2012). The *humifusa* clade has both diploid and polyploid members in southeastern and southwestern US, but northern populations are exclusively polyploid (Majure et al. 2012). Majure et al. (2012) suggest that southeastern and southwestern U.S. served as glacial refugia and the polyploids spread northward following the Wisconsin maximum and that polyploids may have formed as a result of repeated contact between the two southern refugia during the oscillating glacial and interglacial periods. They note that while the ability of northern populations to withstand cold temperatures has been documented, the cold tolerance of diploid taxa is untested and unknown, though some of the northern polyploid populations may be more cold resistant than the diploid taxa they likely developed from (Majure et al. 2012).

Antithetically, higher ploidy levels means larger cells (Masterson 1994; Gorelick 2009), which makes freeze tolerance less likely insofar as it becomes more difficult to quickly move water out of large cells than small cells. But polyploidy is often correlated with geographical parthenogenesis (Vandel 1928) and polyploidy seems to be neither adaptive nor necessarily maladaptive (Gorelick and Olson 2013). What is striking here is that not all cactus species may be purging water from their cells in autumn, as indicated by the turgid state of winter shoots of *Maihuenia*, *Coryphantha*, and *Pediocactus* in Ottawa. And those that do become less turgid in autumn, such as the Opuntioideae, may still retain lots of water in their cells because of cell size. Even *Opuntia fragilis* after cold acclimation is still three-quarters water and one-quarter dry weight

$$\left(\frac{2.63}{1 + 2.63} = 0.725 \right) \text{ (Ishikawa and Gusta 1996).}$$

CONCLUSIONS

More cactus species can live and survive unassisted through Ottawa's very cold winters than was currently recognized. We created a list of twenty species that are known to survive in

Ottawa, demonstrating that there are clearly adaptations for survival of extreme winter climates in the family. We also reported some perhaps surprising failures of species that we expected would be successful. In many cases the successful species are low-lying ones that are able to survive Ottawa's winters. In some cases, even species from native climates where success in Ottawa would seem improbable at the outset survived, such as species endemic to west Texas and southern New Mexico (*Coryphantha sneedii*, *Opuntia arenaria*). Some climatic insulation from snow cover is likely. We note that these specimens were grown in fairly uncontrolled conditions in Ottawa.

In terms of geography and weather, the closest published list of cold-hardy cacti was from central Connecticut (Spain 1997). But Spain (1997) reported very different results from us. Spain (1997) claimed that the most cold-hardy cactus in central Connecticut was *Coryphantha missouriensis*, a plant that we had difficulties with in Ottawa. By contrast, Spain (1997) reported that *Coryphantha sneedii* and *Pediocactus simpsonii* were only marginally hardy in Connecticut, yet those two species and *Pediocactus knowltonii* seem to be the most cold-hardy Cactoideae in Ottawa. Spain (1997) claimed to have never been successful with any South American native cacti grown outdoors in Connecticut, but we have successfully grown both species of *Maihuenia* in Ottawa for several years. The differences between his results and ours may be due to his cultivating different clones from what we have, noting that there is no doubt that he is a far better horticulturist than we are. For instance, the clone of *Maihuenia poeppigii* that has done so well in Ottawa was from a plant collected at 1650 m elevation, which is modestly high for a species that ranges from sea level to 2200 m, albeit rarely over 2000 m (Leuenberger 1997).

We considered why Colorado has so many more native species than eastern Ontario, despite both having similar winter temperatures. Possible reasons for more species in Colorado may be related to basic geographic considerations such as potential source regions. Colorado is far closer to one of the main diversity centers of the Cactaceae, i.e., Mexico (Ortega-Baes and Godinez-Alvarez 2006); Mexico has the highest number of cactus species of any country (660 species, 46 genera), and the highest number of endemics (Ortega-Baes and Godinez-Alvarez 2006). Far fewer species are found in the northern United States along the Canadian border. Species occurrence and abundance is directly a function of migration distance. Other possible reasons for the paucity of cacti in Eastern Ontario include that winter temperatures are colder in Ottawa than Colorado Springs. Snow coverage may be beneficial, but perhaps snow coverage, while far

greater in Ottawa than in Colorado, is still sufficiently intermittent across eastern Ontario in space and/or in time, which could limit dispersal of species into the region that cannot withstand Canadian winters without more reliable snow coverage. However this point is uncertain because Colorado's winter temperatures are only somewhat warmer than Ottawa's and snow cover appears to be inconsequential in Colorado Springs (e.g., Table 2). There is also the possibility that the principal factor(s) affecting cold-tolerance will be different in different geographic regions. Thus, Eric Ribbens (personal communication) suspects that east of the 95th meridian, where it is relatively wet, *Opuntia fragilis* is limited in the southern part of its range by too many freeze-thaw cycles for the plant (not necessarily number of freeze-thaw cycles for the ambient air temperature above any snow). Thus the southern range limit east of the Missouri River is at about 42°N in northeastern Iowa and northwestern Illinois. And the cladodes on many of these plants, which are few and far between, in Iowa and Jo Daviess County, Illinois, are necrotic, with roughly 20% of the cladodes in Buchanan County, Iowa being dead (Eric Ribbens, personal communication). By contrast, west of the 100th meridian, where it is much drier, the southern range limit of *O. fragilis* is much farther south and possibly limited by the need for cold in winter. Out west, the southern range limit of *O. fragilis* is about 36°N in northeastern Arizona, northwestern New Mexico and the Texas panhandle (Correll & Johnson 1970; Pinkava 2004; Ribbens 2008). Plants at the southern edge of the range west of the 100th meridian usually look healthy. And, if *O. fragilis* var. *brachyarthra* (Englemann & Bigelow) J.M. Coulter is considered a valid form of this species, then the species range extends as far south as 32°40'N in southern Pinal County, near San Manuel, Arizona (Benson 1982). Also out west, at the northern range limit of all cacti, near the towns of Fort St. John, British Columbia and Peace River, Alberta, *Opuntia fragilis* is apparently abundant and healthy (Bernshaw and Bernshaw 1984; Gorelick 2015).

Phylogeny does not appear to play a role in winter survivorship of cacti. Perhaps microsite availability and dispersal ability to suitable habitats is important. Many cactus species, even those native to mesic environments, are distributed in sunny, well-drained, xeric microsites, without occupying vast expanses of their natural 'range'. The list of twenty hardy cactus species we present here is based on our experience with select species. There are other species, such as some high-altitude cacti that may be able to survive in Ottawa, such as *Tumilla corrugata* (Salm-Dyck) D.H. Hunt & Iliff and *Maihueiopsis glomerata* (Haw.) R. Kiesling, but these have not yet been

tested. Many of the high elevation cactus species from Argentina and neighboring countries, such as *Oreocereus* (A. Berger) Riccob., perish with even modest amounts of precipitation (Kiesling 1987). But still some Andean and Patagonian cacti might be worth trying to cultivate in Ottawa and other cold, wet climates in an attempt to see what the climatological limits for these plants really are.

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